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RESISTANCE OF DOUGLAS-FIR TO WESTERN SPRUCE BUDWORM: RESULTS OF A PRELIMINARY PROGENY TEST

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ABSTRACT

Second- and third-instar larvae of Choristoneura occidentalis *placed on 3-month-old* Pseudotsuga menziesii *var.* glauca *seedlings from seven different stands dispersed over all test seedlings and exhibited a feeding preference. Reduced feeding relative to the test mean was observed on progeny from a stand that has survived a long-term and severe budworm outbreak. Within-family patterns of variation were much like those observed for other traits of inland Douglas-fir. Larval dispersion appeared to be greatly influenced by expression of highly developed territorial behavior that included territorial display by larvae established on feeding sites and a common response by the intruding larvae.*

KEYWORDS: Douglas-fir, western spruce budworm, insect resistance of conifers, insect territorial behavior.

A characteristic feature of severe budworm epidemics in Canadian spruce-fir forests is selective mortality. Typically, mortality is lower in white spruce (*Picea glauca* [Moench] Voss) than it is in balsam fir (*Abies balsamea* [L.] Mill.) (Ghent et al. 1957), but little data are readily available on the actual percentage of mature stems per acre surviving. In one case, 20 percent of the merchantable balsam fir

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survived 7 years of intense defoliation by budworm (Blais 1958). In another case, mortality typical of merchantable balsam fir, was said to be 97 percent (Blais 1954). Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [(Bessn.] Franco) growing in the Northern Rocky Mountain area of Montana also exhibited differential survivability (Johnson and Denton 1975). Thus, one can say with confidence that both eastern spruce budworm (*Choristoneura fumiferana* [(Clem] Freeman) and western spruce budworm (*C. occidentalis* Freeman) fails to kill all members of its available and preferred host population during severe epidemics. This phenotypic difference could be due to chance variation associated with tree condition and location or it could be due to genetic variation for resistance. Much evidence exists indicating that genetic interaction can coevolve between insects and their food hosts (Price 1977, van Emden 1973, Gilbert and Rowen 1975). So it is reasonable to hypothesize that budworm was involved in the selective mortality. Since "one must suppose that any agent that selectively destroys genotypes, populations, or whole species as effectively as epidemic disease surely has played a role in the evolution of modern faunae and florae" (Harlan 1976), a reasonable conclusion is that budworm and Douglas-fir could have coevolved a genetic interaction; furthermore, if they have, the selective destruction is generally a two-way affair where the prolonged tug-of-war escalates defenses of both sides, many times, and results in a highly complex coevolved genetic interaction that must be maintained to prevent drastic reduction of fitness (Price 1977). The presence of inherited resistance in the budworm:Douglas-fir system would signal the existence of a coevolutionary interaction and then all the principles applying to such systems would apply to the budworm:Douglas-fir system as well.

The presence of a coevolved system means that if Douglas-fir is to be managed in areas where budworm is a potential problem, an integrated control program that is based on an understanding of the genetic interaction is essential to manage spruce budworm. And budworm appears to be a potential, if not current, problem over most of the range of Douglas-fir (Stehr 1967). Much evidence generated in the development of integrated control strategies for pests (including insects) of agricultural crops shows that an element of prime importance is the genetic interaction of the host population and the pest population (Tummola and Haynes 1977, Kogan 1975). Thus, a basic piece of information needed for the development of a budworm control strategy is the role genetic interaction plays in the relationship between the budworm and Douglas-fir.

The purpose of this paper is to report results from a preliminary progeny test of Douglas-fir seedlings exposed to budworm feeding during their first growing season. The experiment was designed to provide a preliminary test of the following hypothesis: If phenotypic differences in defoliation of Douglas-fir by western spruce budworm are due in part to a coevolved genetic interaction, then open-pollinated progeny obtained from various stands and trees within stands should have a significant amount of variation due to stands or maternal trees.

MATERIALS AND METHODS

Wind-pollinated seeds were collected from several Douglas-fir trees, growing in each of 23 stands in 1969 (Rehfeldt, in press). In early 1978, seed remained for six or seven trees from each of seven stands. These seeds were stratified and then planted in standard pine cells in March 1978. The stand locations and descriptions are given in table 1. On June 6, 1978, several hundred second- and third-instar larvae were collected from the lower portion of the Little Joe drainage near St. Regis, Montana. Larvae were collected by removal of branch tips of Douglas-fir containing entrenched larvae. Branch tips were placed in plastic bags and then transported back to Moscow, Idaho, in ice chests containing ice. The materials were left on ice overnight and larvae were distributed to the 3-month-old Douglas-fir seedlings (average height = 57.8 mm) on the morning of June 7.

Table 1.--*Location and budworm damage status of Douglas-fir stands at time of seed collection in 1969*

Stand	Location	Budworm levels
1	Priest River Experimental Forest, Idaho	No obvious damage
2	Meadow Creek, Nezperce National Forest, Idaho	No obvious damage
3	Idaho Creek, Flathead National Forest, Mont.	No obvious damage
4	Lost Horse Creek, Hamilton, Mont.	Light damage
8	Nez Perce Creek, southwest Hamilton, Mont.	Heavy damage, many trees with crowns gone, current epidemic
20	Honeymoon Creek, Thompson Falls, Mont.	No obvious damage
23	Cooper Creek, east of Wallace, Idaho	No obvious damage

Four to eight seedlings from each of the seven half-sib families were placed at random in a 200 cell pine-cell rack. The minimum number of seedlings per stand was 24 (4 seedlings of each of 6 families) and the maximum was 34. Next, 200 of the second- and third-instar larvae were placed on the materials, one to a seedling, and then observed closely for 1 week. Notes were taken on general behavior of the larvae for 1 week, and after 3 weeks the seedlings were taken from their random position and rearranged by stand and mother tree. At this time, degree of defoliation was estimated as percent of available foliage consumed on each seedling. Independent estimates of damage were obtained by two researchers and were averaged to obtain a score for each individual seedling. Each seedling was ranked on a scale from 1 to 10 as follows: An estimated percentage defoliation of 0 to 10 was scored as 1 and so on up to 91 to 100 percent being scored as 10. The scores were subjected to analysis of variance according to Snedecor (1956). Variation among families for defoliation was analyzed by chi-square as was percentage of seedlings from a stand exhibiting bud damage resulting from budworm feeding.

RESULTS

Dispersion of the larvae on the 1-0 Douglas-fir seedlings was most complete. Even though one larva was placed on each tree, most did not stay where placed. The larvae remained very active for about 10 days at which time all those not establishing permanent feeding sites had been lost by simply crawling from the pine cell rack. The number of established larvae (pupated) was not recorded in this preliminary test, but it is known to have been about 10. On certain trees larvae built shelters very quickly by webbing together needles or just spinning a shelter entirely from silk. In other cases larvae were placed on a given tree upwards to 50 times but no shelters or feeding ever occurred on that tree. On other trees many different larvae tried repeatedly to establish feeding sites, but in the end none stayed. In the beginning all larvae that attempted to spin shelters did so at the tips of the trees; however, after 10 days a few larvae settled in the lower parts of the first-year crowns and fed to pupation.

During the dispersion process of the second- and third-instar larvae, the following territorial behavior patterns were observed: (1) Display by the individual occupying the territory (a shelter of his construction), and (2) a quick and uniform response by the intruder. Typically, when an active larva in a shelter was approached by a wandering larva, the established larvae would display by thumping its posterior on its shelter floor. At times, this motion was so violent that the entire seedling would shake. Occasionally, the established larva would also "stamp its feet" rather than use its posterior or do both, but not at the same time. Either display generally elicited the same reaction in the approaching larva. Upon receipt of an assumed message, the intruding larva would quickly drop from the area. Since the intruder was usually aligned with a needle, most often it would simply crawl to the end of a needle and spin down.

The analysis of variance showed a significant main effect (5 percent level) due to stands (table 2). Mean values of progeny defoliation (table 3) showed that stand 8 appeared to be different. Progeny from stand 8 trees incurred about two-thirds the defoliation of the average for the entire test and about one-half as much as the most highly defoliated progeny.

Table 2.--*ANOVA of defoliation by* Choristoneura occidentalis *of first-year Douglas-fir seedlings*

Source	d.f.	SS	M.S.	F
Stands	6	125.97	21.00	2.24*
Seedlings/stand	193	1809.87	9.38	
Total	199			

*Significant at 5-percent level.

Table 3.--*Average defoliation rating and bud damage resulting from* C. occidentalis *feeding on a Douglas-fir progeny test*

Stand	Number seedlings	Average defoliation rating	Percent debudded	Budworm status at seed collection
1	34	3.38	0.94	No obvious damage
2	28	5.18	.89	No obvious damage
3	31	3.52	.58	No obvious damage
4	28	3.61	.75	Light damage
8	31	2.55	.65	Very severe damage
20	24	4.58	.96	No obvious damage
23	24	3.58	.75	No obvious damage
Totals	200	3.73	.79	

Percent debudded:
χ^2 = 18.06
d.f. = 6
Probability of larger χ^2 = 0.01

Variation among stands in the percentage of buds damaged also was significant. The lowest amount of damage was 58 percent and the highest was 96 percent (table 3).

Progenies of individual trees within stands also exhibited great variation in defoliation (tables 4 and 5). Families from stand 8 differed significantly from family to family, whereas families from stand 2, the most susceptible stand, did not.

Table 4.--C. occidentalis *defoliation rating of progeny from individual Douglas-fir trees exhibiting full crown during a severe budworm outbreak (stand 8)*

Cone bearing tree	Seedling defoliation rating				ΣX	$\bar{X}$	ΣX^2	χ^2
9	1	1	1	7	10	2.5	52	10
5	9	3	7	1	20	5.0	140	8
4	7	1	1	1	10	2.5	52	10
8	1	1	1	1	4	1.0	4	0
3	4	2	1	1	8	2.0	22	3
6	1	1	2	1	5	1.25	7	4
10	3	1	1	1	6	1.5	12	2
Totals[1]					63	9.0	174	37

All trees (pooled):
χ^2 = 37.0
d.f. = 21
Probability of larger χ^2 = 0.025

Individual cone bearing trees:
χ^2 = 19.33
d.f. = 6
Probability of larger χ^2 = 0.005

[1]Calculations according to Snedecor (1956, p. 234).

Table 5.--C. occidentalis *defoliation rating of progeny from individual Douglas-fir trees growing in stand free of budworm (stand 2)*

Cone bearing tree	Seedling defoliation rating				ΣX	$\bar{X}$	ΣX^2	χ^2
23	5	5	8	5	23	5.75	139	1.17
28	7	5	1	10	23	5.75	175	7.43
29	9	1	8	3	21	5.25	155	8.52
12	10	9	1	2	22	5.50	186	11.82
14	2	3	3	9	17	4.25	103	7.24
16	1	9	9	10	29	7.25	263	7.28
20	3	3	2	2	10	2.50	26	.40
Totals[1]					145	20.71	209.43	43.86

All trees (pooled):
χ^2 = 43.86
d.f. = 21
Probability of larger χ^2 = 0.005

Individual cone bearing trees:
χ^2 = 10.11
d.f. = 6
Probability of larger χ^2 = 0.20

[1]Calculations according to Snedecor (1956, p. 234).

DISCUSSION

The two significant results of this preliminary test are (1) western spruce budworm can be easily collected and distributed to Douglas-fir progeny tests and made to feed sufficiently to establish data, and (2) genetic variation in defoliation among stands suggests that feeding preference of budworm is apparently influenced by an inherited factor, or factors, in the Douglas-fir host. This conclusion lends tentative support to the idea that budworm and Douglas-fir have coevolved an interactive genetic system, as does the fact that of the seven stands tested only stand 8 has been exposed to recent heavy defoliation by budworm. Trees supplying seed from this stand were those that were being relatively lightly defoliated. Also, these same stands exhibited patterns of variation for several other adaptive traits (Rehfeldt, in press) that were very similar to those reported in this paper.

The great amount of seedling-to-seedling variation (tables 4 and 5) in level of defoliation within maternal populations was not unexpected. Rehfeldt (in press) reported high amounts of this kind of variablity for six physical traits of inland Douglas-fir. Although the variation within maternal populations could be due to erratic feeding behavior, it is just as likely due to within-family genetic variance. Also, we know that larvae visited all the seedlings because several to numerous strands of silk were observed on the needles of all seedlings and budworm larvae are known to spin silk wherever they go (Harvey 1957). One certainly must concede the possibility that the variation within families is due, in large part, to genetic variation along with the stand related genetic variation. A larger test is certainly called for.

The amount of budworm feeding on buds varied with stand, but stand 8 exhibited the second lowest level (table 3). The lowest level was recorded for stand 3, which was free (no obvious damage) of budworm during the seed collection period. Progeny from stands similar to stand 3 exhibited as high as 96 percent bud feeding. These results indicate that the budworm:Douglas-fir interaction is complex.

The territorial behavior seemed to be most effective at insuring maximum dispersal of the larvae and could play an important role in population regulation of budworm (Klomp 1964). Knowledge of this behavior could also be important in designing future progeny tests.

CONCLUSIONS

Results of this preliminary test suggest that inheritance may be involved in the modification of *C. occidentalis* behavior by Douglas-fir genotypes. Thus, the budworm: Douglas-fir system apparently does contain coevolved genetic interaction. *Choristoneura occidentalis* can be manipulated in a laboratory setting to feed on Douglas-fir progeny tests. Methods can be developed to measure defoliation and other kinds of damage. Large numbers of larvae can be easily collected and quickly distributed over the materials to be tested. Finally, second- and third-instar larvae are largely self-dispersing, provided population levels exceed available feeding sites, due to the territorial behavior of *C. occidentalis*.

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